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### A NEW SPIRANTHES FROM THE GRASSLANDS OF CENTRAL NORTH AMERICA

BY  
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The genus *Spiranthes* L. C. Rich. is highly complex and in eastern North America has caused some confusion among taxonomists and others who have had cause to determine occasional specimens. Many species are with difficulty separated from their allies, and apparent hybrids occur with sufficient frequency to obscure specific distinctions. Among the species most notorious for such behavior is *S. cernua* (L.) L. C. Rich. This species comprises various ecological and morphological races, at least some of which appear to intergrade and hybridize with other species. *Spiranthes cernua* has needed definitive study, but wide field experience is a prerequisite for such an undertaking, and, thus far, no one has attempted to clarify the situation. At present, two varieties in addition to the heterogeneous assemblage considered typical are frequently recognized.

Variety *odorata* (Nutt.) Correll differs from more typical *S. cernua* in its rhombic-ovate lip, stoloniferous roots, and its occurrence principally in coastal plain swamps. It is often appreciably more robust and foliose than typical *S. cernua*. This taxon has historically been treated as

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a distinct species, and taxonomists have not been unanimous in accepting Correll's treatment.

Variety *ochroleuca* (Rydb.) Ames is poorly understood, and there has been much uncertainty concerning its status. It may be distinguished by its yellowish, strongly fragrant flowers and long floral bracts, the lower ones of which exceed the flowers in length. It is said to produce monoembryonic seeds, in contrast to the polyembryony characteristic of typical *S. cernua*. Its distribution has been variously restricted to east of the Appalachians or expanded to include the entire range of the species.

Other species and varieties have been proposed in this complex, but all have been referable, at least in the absence of a thorough study of possible ecotypic differentiation in this species, to the var. *cernua* complex, to var. *odorata*, or to other species.

It is thus only with caution that one would describe a new taxon in this complex, for the danger of introducing additional confusion is great. However, if progress is to be made in our understanding of the group, some risk must be taken, and, in the hope that it will aid in a clarification of the situation, I am describing the following species. My understanding of this species and the *S. cernua* complex as a whole is based on fourteen years of field experience principally in Illinois and surrounding areas and on the study of hundreds of herbarium specimens from all parts of the range of the complex. During this period, the habitats of the complex were studied in detail, and three habitat groups emerged. Further study revealed that morphologically distinct populations were restricted to the various habitats, thus indicating the presence of taxonomic differentiation within the complex. Two of the three evident taxa are here considered to be ecotypes of *S. cernua*. The third, however, has proven distinct enough to warrant specific rank.

**Spiranthes magnicamporum** *Sheviak spec. nov.*

Herba erecta, infra glabra, supra pubescens, copiosa cum trichomis capitatis, 15–57 cm. alta. Radices tuberoso-crassae, usque ad 8 mm. in diametro. Folia omnia radicalia, fugacia, lineari-lanceolata, basi cuneata, acuta, usque ad 12 mm. lata, 14 cm. longa. Caulis gracilis ad lacuno-crassa, 1.5–7 mm. in diametro, aliquot bracteis vaginantibus instructa. Spica densa, 15–28 mm. in diametro, 4–18 cm. longa. Phyllotaxis  $\frac{1}{3}$  vel rariter  $\frac{1}{4}$ ; orthostichies saepe in forma spirale. Bracteae floriferae ovatae, attenuatae vel saepe acuminatae, 10–30 mm. longae. Flores albi ad eborei, labelli pars centralis saepe flava, valde cumarino-aromatici: segmentis perianthii extus pubescentibus. Sepalum dorsale lanceolatum, acutum, 7–11 mm. longum, 1.5–3 mm. latum; sepala lateralia libera, late patentia ad rariter laxe incurvata, lineari-lanceolata ad lineari-oblonga, acuminata ad obtusa, 7–11 mm. longa, 1–2 mm. lata. Petala sepalo dorsale adhaerentia, linearia, acuminata, 7–10 mm. longa, fere 1 mm. lata. Labellum oblongo-ovatum ad rhombico-ovatum vel rariter fere triangulare, potius aequaliter arcuatum sed apice saepe abrupte reflexum; sine dilatatione basale vel constrictione mediane; margine integro vel parte quarta apicole dentato, vix crispo; 7–11 mm. longum, 3.5–6 mm. latum; calli basales prominentes, pubescentes.

**Typus:** *R. A. Evers* 98153. “Hill prairie, 3.5 mi., S., of Eldred, Greene Co., Illinois, Oct. 10, 1968.” (specimen “a”). *Typus in* ILLS.

*Other characteristic, noteworthy collections include:*

*R. T. Rexroat* 4411. “Oct. 2, 1957. Scott Co., Illinois. High loess hillside. Fls. very fragrant.” (ISM).

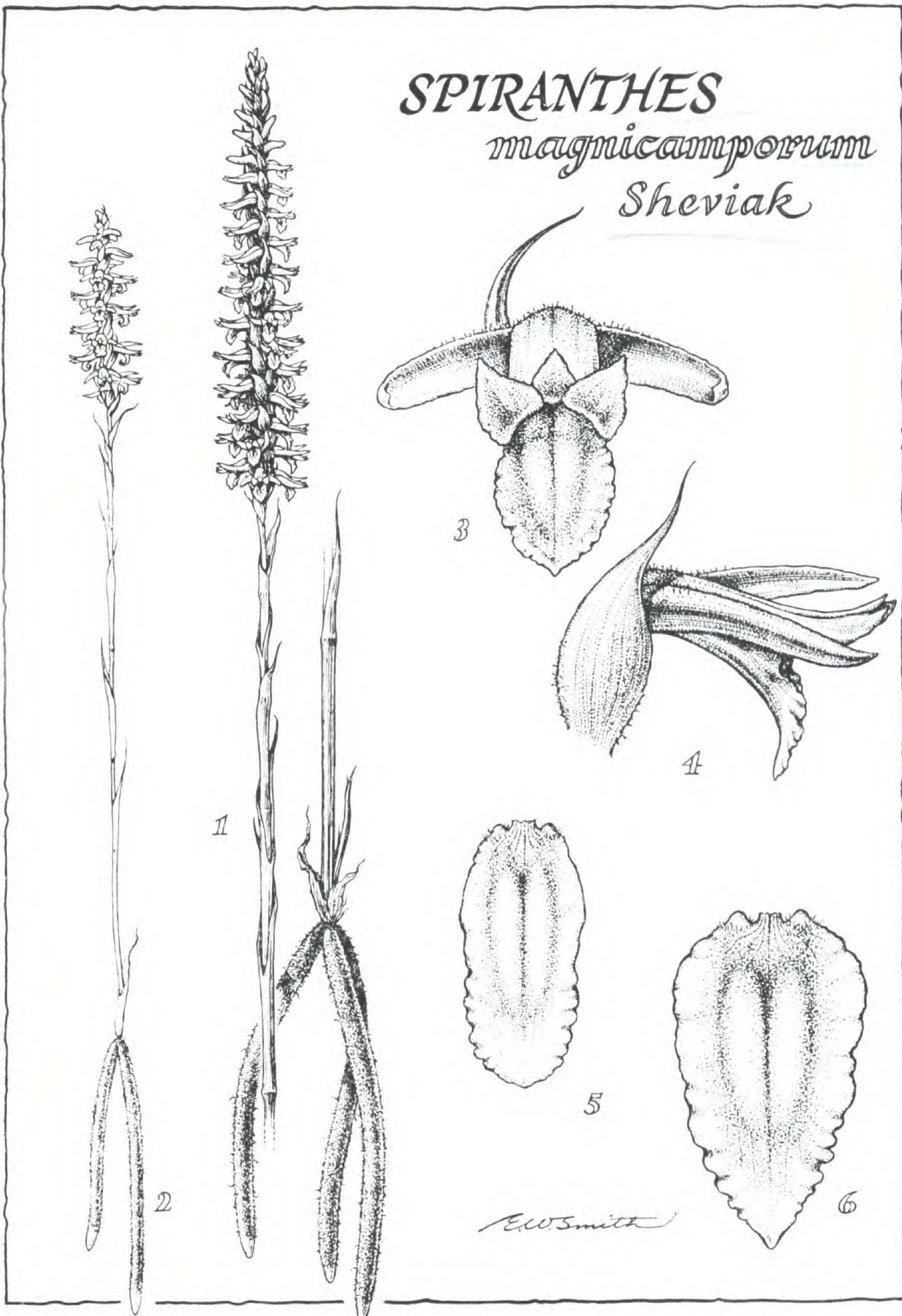
*C. J. Sheviak* 352. “Orchidaceae of Illinois: 69-11-07-04: very abundant in grazed hill prairie. with *An-*

*dropogon scoparius*, *Linum sulcatum*, *Aster azureus*, *Petalostemum purpureum*." full sun. soil dry calcareous loess. Bland Hill Prairie, 3.2 miles N. of Eldred, Greene County. 7 November 1969." (To be deposited at ILL.)

*Spiranthes magnicamporum* occurs on dry prairies and related grasslands from northwestern Indiana onto the Great Plains (hence the specific epithet "*magnicamporum*", a direct translation of "of the Great Plains") with disjunct populations on the prairies of western Ohio and the black belt of Mississippi and Alabama. It ranges from Texas north to at least North Dakota.

*Spiranthes magnicamporum* differs from *S. cernua* var. *cernua* in several characters. The flowers of well developed plants of *S. magnicamporum* are larger than those of var. *cernua*, the perianth often exceeding 1 cm. in length. The lip of *S. magnicamporum* is uniformly oblong-ovate to rhombic-ovate, characteristically without the dilated base usually present in var. *cernua*. In var. *cernua*, the apical portion of the lip is also occasionally dilated, thus producing a lip with a median constriction. These dilations are nearly always absent in typical *S. magnicamporum*. The central portion of the lip of typical *S. magnicamporum* always supports a prominent thickening that is distinct even in boiled herbarium material. This is a variable character in *S. cernua* and is often absent. Crisping of the lip is less marked in *S. magnicamporum* than in var. *cernua*, and the laceration of the lip is suppressed, the margin often quite entire or the apical quarter merely dentate. Lateral sepals are free and widely spreading to rarely loosely incurved or often ascending, unlike those of var. *cernua*, which closely parallel the petals and join to form a hood. The flowers of *S. magnicamporum* are often more nearly cream-colored than the white usual in var. *cernua*, and the central thicken-

*SPIRANTHES*  
*magnicamporum*  
Sheviak



*Spiranthes magnicamporum* Sheviak. 1 and 2, plants, one half natural size. 3, flower and tip of bract, front view, three times natural size. 4, flower and bract, side view, three times natural size. 5 and 6, lips, somewhat flattened, four times natural size.

Drawn by ELMER W. SMITH

ing of the lip is often yellow. They are strongly fragrant with the scent of coumarin, in contrast to the flowers of var. *cernua*, which, in the geographical zone of contact in the midwest, at least, are generally scentless, or, when aromatic, exhibit usually but a faint fragrance strikingly like the scent of fresh *Cypripedium* roots. In well developed specimens of the two taxa, the inflorescences are strikingly different due to differences in the orientation and shape of the flowers. The nodding of var. *cernua* is accentuated by a general curvature of the dorsal sepal, whereas in *S. magnicamporum* this segment is arcuate only near the base. The orientation of the lip also varies: in *S. magnicamporum* it is rather uniformly arcuate along its length, although the apex is often abruptly reflexed, whereas in var. *cernua* the lip is often rather geniculate at about the middle. These differences in flower shape and orientation lend different aspects to their respective inflorescences. In var. *cernua*, the general impression is of an ornate inflorescence, an impression often accentuated by the reflexed tips of the sepals and petals. In *S. magnicamporum*, the more linearly organized flowers produce a strikingly scalariform inflorescence. The populations of typical *S. magnicamporum* which I have studied produce monoembryonic seeds, although polyembryony appears to be frequent in some areas. The seeds of this species tend to be short and broad, generally oblong-quadrate and truncate but occasionally vary toward the more fusiform seeds of var. *cernua*. The living plants of typical *S. magnicamporum* available for study were not apogamous, whereas I have found that var. *cernua* characteristically sets seed without pollination.

These taxa vary vegetatively as well. A salient feature of *S. magnicamporum* is the absence of leaves at anthesis. These senesce two to several weeks before the inflorescence appears. In var. *cernua*, however, they persist dur-

ing anthesis or, under adverse conditions, senesce as the inflorescence develops. This behavior is genetically determined and cannot be altered under cultivation. The roots of *S. magnicamporum* also tend to differ from those of *S. cernua* in their greater tuberosity (the smaller plant illustrated in the figure possessed abnormally slender roots).

Many of these characters vary with the vigor of the plant and are sometimes difficult to utilize in depauperate or stunted individuals. It is of great significance that cultivation increases the expression of typical characteristics of the two species, even in specimens of previously obscure relationships. Under more nearly uniform cultural conditions, many previously similar individuals of the two species diverge greatly in phenotype, thus supporting the separation here proposed, but further indicating the difficulty inherent with the group.

What is here described as *Spiranthes magnicamporum* has also been confused with var. *ochroleuca* and var. *odorata*. It is not referable to var. *ochroleuca*, as the original description of *Gyrostachys ochroleuca* (the type specimen cannot be located) refers to "lower stem leaves" which do not occur in *S. magnicamporum*. The flowers of var. *ochroleuca* are also evidently smaller than those typical of *S. magnicamporum*. Furthermore, *S. magnicamporum* is a distinctly western species and apparently does not occur east of western Ohio, where it is disjunct. The type of var. *ochroleuca*, however, was collected in New England.

Unfortunately, I have not seen var. *odorata* in the field and do not have a satisfactory understanding of it. *Spiranthes magnicamporum*, however, appears to be closely allied to it and may represent a northwestern, dry, exposed-site counterpart. The aspect of the inflorescences and some floral details of both of these taxa are notably similar. They differ in persistence and location

of leaves and in the nature of the roots. Both of these characters are genetically determined in *S. magnicamporum*, and development under wet conditions does not alter them. Even in two specimens from calcareous hanging fens in Illinois the leaves remained fugacious and the roots tuberous.

In general, it appears that *S. magnicamporum* is a western, prairie counterpart of *S. cernua*. Although not allopatric (indeed, *S. cernua* occurs further west than *S. magnicamporum* in several areas), *S. magnicamporum* is the more prevalent in the west and is better adapted to the droughty conditions of the area than is *S. cernua*, which often relies upon local abundance of moisture for its survival.

The two species, are, however, truly sympatric only on rare occasions, for even where occurring at the same station these species are spatially isolated by ecological factors. Of the two ecotypes of var. *cernua* that I have been able to distinguish in the Illinois region, one occurring principally in moist sand prairie, the other in dry open woods and old fields on finer textured soils, usually only the former occurs with *S. magnicamporum*. At such stations *S. magnicamporum* occupies the dry ridge tops and *S. cernua* the wetter swales. Both of these taxa occur in calcareous hanging fens, but *S. magnicamporum* does so very rarely, only two such stations being known, and I have never seen them associated at such a site. *Spiranthes magnicamporum* is further isolated from this sand prairie ecotype of *S. cernua*, at least in the southern Lake Michigan region, by season, as these *S. cernua* populations bloom from mid-August to mid-September, whereas in *S. magnicamporum* anthesis is initiated usually in mid-September and continues into October. Floral fragrance (which is lacking in this ecotype of *S. cernua*) may likewise serve to isolate these taxa.



*Spiranthes magnicamporum* is also apparently isolated from the old field-open woodland ecotype of *S. cernua* by edaphic factors. In my experience, *S. magnicamporum* has proven to be a distinct calciphile, whereas the old field ecotype of *S. cernua* occupies strictly acidic soils. Only two specimens of *S. magnicamporum* are known from areas of generally acidic soils, but the precise natures of these stations are unknown. Both could be from localized calcareous areas which occur in the regions involved. Floral fragrance probably further isolates these taxa. Pollination studies (which were not possible during my study) would be most useful in this group.

These two ecotypes of *S. cernua* have also proven to be genetically isolated from *S. magnicamporum*, at least in the small sample available for study. Four plants of *S. magnicamporum* from two localities in Illinois (Greene and Lake counties) were crossed with three plants of *S. cernua*, two of the old field ecotype from two localities (Pope County, Illinois and Fountain County, Indiana) and one of the sand prairie ecotype (Kankakee County, Illinois). A total of twenty crosses were made using *S. magnicamporum* as the pistillate parent (because of the apogamous nature of *S. cernua*) and flowers of several ages. Absolutely no seed was obtained from these crosses. It should be noted, however, that because of differences in period of anthesis, the pollen from the sand prairie ecotype of *S. cernua* was stored for two weeks before use.

It is clear that this apparent isolation does, in fact, occur. It is indicated by the situation in a region of dune and swale topography along the Lake Michigan shore in Lake County, Illinois. Here *S. cernua* (sand prairie ecotype) occurs by the hundreds in low sand prairie swales. Infrequent plants of *S. magnicamporum* are scattered on the xeric ridges. I have never found an intermediate plant in the field, despite intensive search, and

have seen only one or two preserved specimens from this locality that showed signs of intergradation.

Apparently, the differences in edaphic requirements of *S. magnicamporum* and the old field ecotype of *S. cernua* normally preclude their close association, but I have recently learned of a station that supports both taxa. The small number of specimens that I have seen from this locality do not allow definitive work, but it seems that the two species are maintaining their integrities at the site. The edaphic nature of the area that allows such an admixture is unfortunately unknown.

Because of the several apparent isolating mechanisms present between *S. cernua* and *S. magnicamporum* and the evidently greatly restricted gene exchange, I consider them to be distinct species.

Nevertheless, it is apparent that some gene exchange has occurred. Particularly in sand deposits, intermediate specimens may occasionally be found. In nearly all such cases of which I am aware, however, such plants are from disturbed sites; drainage, intensive pasturage, and excavation are common factors in Illinois. Fewer intermediates are found in areas where the *S. cernua* influence must have been contributed by the old field ecotype, and only limited introgression is indicated.

One major intermediate race is known, however, and it complicates the situation. In northern Illinois, there occur, in low black-soil prairie, populations somewhat intermediate between *S. magnicamporum* and the sand prairie *S. cernua*. It appears that rare crosses between these taxa have produced a race that occupies a hybrid habitat. This race differs from typical *S. magnicamporum* in the presence of a basal dilation of the lip and the poor development or even complete absence of the central thickening. I have seen only two live plants of this taxon in bloom, and these were apogamous. Although scented

as in typical *S. magnicamporum*, the intensity of fragrance was less than in typical plants of this species. Specimens of this race are, however, still recognizable as *S. magnicamporum* by the aspect of the inflorescence, the position of the lateral sepals, floral fragrance, the fugacious nature of the leaves, and the tuberosity of the roots.

These plants occupy low calcareous black-soil prairie. They may occur over but a restricted portion of the range of *S. magnicamporum*, and I have recognized them only in northern Illinois. Judging from the numbers of specimens and known stations, this taxon seems to be particularly well represented in the Chicago area, although this observation may reflect irregularities in collecting activity.

It is apparent that these plants are intermediate between *S. cernua* and *S. magnicamporum*. Thus, this race may have arisen as a hybrid between *S. magnicamporum* and the sand prairie *S. cernua*. Evidently a portion of the resulting offspring became established in the edaphically hybrid habitat of low black-soil prairie. The presence of this race outside the range of the sand prairie *S. cernua* in Illinois suggests that this hybrid taxon spread from its point of origin to its present range across northern Illinois. It would appear most likely that the initial hybridization occurred in the Chicago area, where the greatest concentration of populations are to be found and where the necessary juxtaposition of the parents and low black-soil prairie occurs.

It is not clear if a single or several hybridizations were involved in the founding of these populations; indeed, it is possible that similar populations have arisen independently at other localities in the range of *S. magnicamporum*. Nor is the influence of backcrossing known. Variation between the parents occurs, but it is not known if this reflects segregation from a single initial hybrid

gene pool or repeated hybridization. The point is of significance to this work because it affects the taxonomic status of these populations. Because backcrossing is more likely between these plants and *S. magnicamporum* than between them and the usually spatially isolated *S. cernua*, and because the two live plants that I have seen and the majority of herbarium specimens examined appear more characteristic of *S. magnicamporum* than *S. cernua*, in the absence of wider experience with these plants it seems best to treat them as a vaguely defined race of *S. magnicamporum* rather than to consider them in a more definitive manner.

That such hybridization can occur is of interest in addition to its relevance to the problems inherent in determining a specimen in this complex. I have seen a few specimens from east of the range of *S. magnicamporum* that exhibited various characters of this species but which were otherwise referable to *S. cernua*. Occasionally these were collected with normal specimens of the latter species. It would appear that during the xerothermic period *S. magnicamporum* ranged much further east than at present, following the availability of dry prairie. As the climate moderated, this species retreated westward, but some hybridization with *S. cernua* did occur as environmental barriers deteriorated. Genes of *S. magnicamporum* were then thoroughly incorporated in the gene pools of various populations of *S. cernua*, so that now recombination produces rare plants suggesting *S. magnicamporum* in various respects.

It is unfortunately not certain how *S. magnicamporum* behaves with regard to *var. odorata*. I have not had live material of this taxon available for hybridization experiments. Apparently the only contact between the ranges of these taxa is in the black belt. They cannot, however, be truly sympatric because of their different habitat re-

quirements. Furthermore, it is almost inconceivable that they could produce hybrid offspring capable of finding suitable habitat for survival even if they were associated somewhat closely. Indeed, the fact that these two taxa remain distinct in this area supports their taxonomic separation.

It should be noted that, although this work represents only a beginning of our understanding of the *S. cernua* complex, it does open an interesting possibility. Much, if not all, of the material from the North and West that has been referred to var. *odorata* is in actuality *S. magnicamporum* or introgressed *S. cernua*. This situation suggests that a re-evaluation of var. *odorata* is in order and may further clarify the status of this and other segregates of the *S. cernua* complex.

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